How do pathogen evolution and host heterogeneity interact in disease emergence?

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Supplementary Material

There are clearly degeneracies in our parameterisation of host heterogeneity. However, it allows us to distinguish factors intrinsic to each host from social factors. It also allows us to understand how these conceptually distinct factors may be able to compensate for one another in the determination of the probability of emergence of a disease.

To understand the source of the degeneracies, we first note that the n^2 independent quantities $R_0^{(ij)}$ completely specify the system (equation (2) in the paper). Our parameterisation however contains $n^2 + 3n - 2$ degrees of freedom; $n - 1$ in η, $n - 1$ in σ, $n - 1$ in f, n^2 in π and one in R_0. We note that η, π and σ appear only in the combination $\beta_{ij} = \eta_i \pi_{ij} \sigma_j$. So immediately we can see that any transformation of η, π or σ that leaves the quantity β_{ij} invariant gives rise to the same matrix $R_0^{(ij)}$ – for instance, uniformly increasing infectivity and decreasing susceptibility by the same factor. The matrix $\boldsymbol{\beta}$ then has n^2 independent parameters, and so the quantity

$$R_0^{(ij)} = N\eta_i f_j \sigma_j \pi_{ij} = N f_j \beta_{ij},$$

is specified by $n^2 + n$ free parameters; n^2 in $\boldsymbol{\beta}$, one in the normalisation factor N (proportional to the R_0 of the population as a whole) and $n - 1$ in f. Now we see that there exists an n-dimensional family of transformations that leave $R_0^{(ij)}$ invariant. One component of this family is the scalar transformation

$$\boldsymbol{\beta} \to \alpha\boldsymbol{\beta}, \;\; N \to N/\alpha,$$

where α is a constant. This simply reflects the fact that η, π and σ are expressed in arbitrary units. The remaining transformations that leave $R_0^{(ij)}$ invariant are specified by

$$f_j \to \tilde{f}_j = \delta_j f_j, \;\; \beta_{ij} \to \tilde{\beta}_{ij} = \frac{1}{\delta_j}\beta_{ij},$$

where the transformation vector δ_i must satisfy the constraint $\sum \tilde{f}_i = 1$ and so has n –1 independent components. Together, α and δ remove n degrees of freedom leaving n^2 as required. This set of symmetries indicates that heterogeneity in recipient qualities (the second index in β_{ij} – susceptibility and mixing, but not infectivity) may be compensated for by changes of host frequencies. In other words, decreasing the frequency of one host type in the population and simultaneously increasing their susceptibility may give identical $R_0^{(ij)}$ and probability of emergence.